

A CRITICAL RESPONSE TO THE PAPER “TOUGH AFRICAN MODELS AND WEAK MIMICS: NEW HORIZONS IN THE EVOLUTION OF BAD TASTE” BY P. DEVRIES PUBLISHED IN THIS JOURNAL, VOL. 57(3), 2003

P. DeVries has published two papers in the last two years about the existence of a strong association between “bad taste” of butterflies and toughness of wings (DeVries 2002, 2003). One of these papers, “Tough African models and weak mimics: new horizons in the evolution of bad taste,” was published in this *Journal* (57: 235-238). Here, I present a critical review of both of DeVries's papers and an opposing point of view.

DeVries postulates that the evolution of “bad taste” (distastefulness) is, in some way, directly connected with the development of tough wings, and that “a toughened wing integument may be a general trait associated with the evolution of distastefulness in butterflies.” He argues that toughness of wings appears to be an essential component of butterfly resistance to bird attacks. He claims that he presented experimental proof of his concept of “a wing toughness spectrum that has evolved in parallel with the palatability spectrum” and that “toughness of the wings makes butterflies resistant to handling by predators.” I fully disagree with these concepts. I consider them the result of conclusions made on the basis of an experimental design that does not mimic natural conditions.

Under the conditions of the experimental design used by Dr. DeVries, a dead butterfly is firmly “fixed in the grip of a clothing peg with all four wings closed in a natural resting position” leaving free only part of the wings. A clip assembly (the artificial metallic beak) is attached to the hind wings distal margin in such a way that the jaw grips the wings of the dead butterfly between veins Cu1 and 2A. Weight is applied on the artificial beak until there is a tear in the wings and the metallic beak, with the applied weight and the part of the torn wing remaining into its grip, falls into a collecting receptacle. This weight determines the wing tear weight (DeVries 2002, 2003). This weight was found to be in the range of many hundreds of times that of the butterfly tested - 40.0 g for the unpalatable *Amauris niavius* (a weight that surpasses that of most insectivorous birds), 15g for *Acraea insignis*, and 7.5 g for the palatable *Bicyclus sfitza* and *Junonia terea*.

Under natural conditions the butterfly is not firmly fixed as it is under the conditions of the experimental design used by DeVries. Usually, when caught by a bird, a butterfly hangs freely, with only one wing fixed by the grip of the beak. The body of the live butterfly

and the remaining three wings remain free. There is practically no weight applied; the weight of the freely hanging butterfly is negligible. Thus, the force responsible for the tear of the wing under natural conditions is the strength applied by the violent struggling of the freely hanging butterfly to escape from the grip of the beak. Obviously, the stronger the butterfly, the higher is the chance the caught wing will sustain a tear and the butterfly will fly away with only relatively small damage to the wing. If the wing breaks under the weight of the insect, a bird could never catch successfully and consume a butterfly. Thus, under natural conditions, the “wing tear weight” (wtw) is the force applied by the struggling butterfly to free itself from the grip of the beak. It is a very dynamic, pulling, tearing force applied under different conditions than those in the experimental design used. It is not a gradual increase of added weight on the firmly fixed wings of a dead butterfly.

If this force could be measured in grams and approximated that of the weight applied under the conditions of the experiment causing a tear in the wing, the experimental design used by DeVries could reflect natural conditions. DeVries (2002, 2003) claims that “by estimating the force necessary to tear wings” his reports “corroborate the hypothesis that wing toughness may be a corollary of unpalatability in butterflies.” However, he does not estimate the force applied on the beak of the bird by the struggling butterfly leading to a tear in the wing at the point where the beak holds the wing. Instead he considers that it is the weight applied on the wing that leads to a tear.

In general, palatable butterflies characteristically have a short, stout fatty body, relatively shorter wings, wide thorax and a fast erratic flight. In contrast, butterflies considered unpalatable are characterized by long slender bodies, elongated wings, narrow thoraxes, fluttering wing beats, and a slow flight in a straight and regular path (Marshall 1909; Chai 1986, 1988; Chai & Srygley 1990; Srygley & Chai 1990; Pinheiro 1996). The flight pattern of palatable butterflies is highly correlated with thoracic muscle mass (Chai & Srygley 1990, Srygley 1994). In fact, most of their wide thoracic cage (85-95% of wet thoracic mass) is filled with massive flight muscles for quick take off, acceleration and increased flight speed (Hocking 1985; Ellington

1991). Evidently, butterflies considered palatable possess a high struggling ability, more strength and thus a better chance to slip out of the beak or escape its grip — leaving the bird with only a small piece of wing in the beak. In contrast, the markedly elongated slender thorax of butterflies considered unpalatable is associated with weaker flight muscles (less muscle mass), which explains their characteristic flight pattern. No doubt, they are less capable of opposing the strong grip of the beak. Evidently, a palatable butterfly, having a low wtw (weaker toughness of the wing), is better protected than a distasteful one from being eaten by a bird by escaping only with a small defect in its wing. Thus, the considered distasteful butterflies, contrary to DeVries's thesis, are less capable of escaping from the grip of the beak, i.e., more vulnerable to predation by birds, despite their higher wtw.

Two questions arise: Why should unpalatable butterflies, despite their supposed strong chemical defense and warning aposematic coloration, evolve wings with a high wtw -- a physical attribute that makes them more vulnerable to predator attack than palatable butterflies which, instead of a chemical defense and warning (aposematic) color patterns for evading a predator, rely on their cryptic color patterns and a fast erratic flight? Why should palatable butterflies with their characteristic fast erratic flight be attacked by birds and comprise their usual diet but unpalatable butterflies, with their characteristically fluttering wing beats, slow flight in a straight and regular path and wings with high wtw, be avoided by predatory birds? It is a paradox that prey that is easy to catch and with a high wtw is avoided and prey that is most difficult to catch and possesses wings with low wtw is preferred by birds and forms part of their regular diet.

I argue that a bird does not reject a butterfly on the basis of aposematic color pattern and a supposed chemical defense, but rather on the basis of a characteristic morphological and behavioral pattern, which provides the bird with a signal whether the prey is actually profitable or unprofitable as a food source (see Kassarov 2003b, c). Only the flight muscles, the reproductive organs, the digestive tract and the abdominal fat have a nutritional value; the remaining chitinous integument, including the wings, is not metabolized. In contrast to the narrow thorax and long slender body of unpalatable butterflies, palatable butterflies characteristically have a wide thorax filled with powerful flight muscles and a stout, fatty abdomen.

It is well known that butterflies considered unpalatable have a tough, very resilient body with a rubbery consistence. Wiklund and Järvi (1982) suggested that, because many aposematic species are tough and diffi-

cult to kill (Cott 1940; Edmunds 1974), body toughness (they do not mention the wings) would reduce the risk of a lethal attack and allow them to escape. Birds are very seldom, if at all, able to attack the butterfly's body directly. The relatively small body is well hidden between the large wings and thus protected by them from a direct attack. This fact is especially true for aerial hawkers, the main bird predators of butterflies, who catch their prey on the wing. To reach the body, the bird has to lose energy first to catch the butterfly and then, as most bird species do, dismember the butterfly (another energy and time-consuming process) before finally swallowing it. Whether the body is tough or not tough does not change the fate of the butterfly; a dismembered butterfly is a dead butterfly. If toughness of the integument protects an insect from being eaten by birds, Coleoptera with their "armored" integument should be the best-protected insects. In fact, these insects belong to the regular diet of birds regardless of whether they are hawkers catching their prey on the wing or terrestrial gleaners.

There are no published data concerning a causal relationship between toughness of the integument and chemical compounds that may render the insect distasteful. Such a relationship could exist if based on a chemical reaction; for example, polymerization of the chemical compound responsible for a chemical defense that leads to hardening of the chitinous integument. It seems highly improbable, however, that chemical compounds that supposedly render a butterfly distasteful could cause the integument to become tough and resilient simultaneously (see Kassarov, 2003a).

Thus, how could toughness (high wing tear weight) of the wing be a "corollary of unpalatability" as DeVries (2002, 2003) postulates? It is rather a corollary of palatability. If there is "an evolutionary correlate between toughness of wings and unpalatability," it is logical to expect that there should be an evolutionary corollary between weakness of wings and palatability. Neither is correct. Chemical defense (distastefulness) of the butterfly and toughness of wings are two attributes that evidently do not act in concert but against each other. The weaker the wing (the lower the wtw), the better the chance the butterfly will escape and vice versa - the tougher the wing, the lower the chance that the butterfly will escape. The only way the butterfly can escape is by the wing breaking at the point where the beak holds it. Thus, low wtw facilitates escape. If the wing does not break, the bird will subdue the butterfly, i.e., the butterfly will be a dead butterfly. If taste is the factor responsible for the rejection of a distasteful butterfly by a bird predator, why should nature cre-

ate conditions for the parallel evolution of a physical attribute (toughness of wing) acting against the supposed chemical defense? The bird's ability to taste a butterfly via beak mark tasting was discussed in detail elsewhere (Kassarov 1999). It was shown that an insectivorous bird is not able to taste a butterfly via beak mark tasting.

There are many more flaws in DeVries's experimental design. Using only a single size artificial metallic beak (10mm x 3.68mm) makes a reliable comparison of wing tear weights in butterflies with different sizes hardly possible. The smaller the wing the larger will be the torn area of the wing in proportion to its size and the lower will be the wtw; the larger the wing, the smaller will be the torn area and the higher the wtw. The smaller the part of wing gripped by the artificial beak, compared to the remaining free part of the wing, the lower will be the wing tear weight. The closer the artificial beak is placed to the periphery of the distal margin of the wing, the weaker will be the measured toughness of the wing (the wtw). For comparable results, an equal part of the artificial bill should grip the wings of the different butterflies tested (for example, 10.0 mm inward from the outer margin of the wing), and, what is more important, an equal part of the wing of the butterflies with a different size tested should be out of the grip of the clothing peg (only one size clothing peg was used). The greater the part of the wings of the firmly held butterfly (with the wings closed in a natural resting position) secured in the jaws of a wooden clothing peg, the higher will be the wtw. For an assessment of the toughness of the wings of different species belonging to different genera, the artificial beak used in the experiment should grip an equal portion of wing. Whether the artificial beak is placed in the space between two veins or in a space including one or more veins affects markedly the value of the wtw. The "vein tear weight" can be expected to be markedly higher than the wing tear weight measured with the beak placed in the space between two veins. The smaller the wing, the smaller is the space between two veins. Using the same size artificial beak and clothing peg leads inevitably to misleading results. DeVries did not use same sized winged butterflies. Thus, the position of the artificial beak on the wing (angle of attachment, amount of wing gripped, etc.) is most important for receiving comparable results. The presentation of the experimental design in the methods section of DeVries's (2002, 2003) papers is very vague, inviting many questions in regard to its reliability.

DeVries (2002, 2003) reports no significant relationship between wing length and wtw among species.

This finding is misleading. It does not reflect the conditions observed in nature. As mentioned above, under his experimental design, the artificial beak is anchored in the space between Cu1 and 2A (hind wings) of the firmly fixed four wings in the jaws of a wooden clothing peg. However, under natural conditions, i.e., the butterfly hanging free (not fixed), held only at the point of the grip of the beak, the length of the wing will play a significant role. The strength of the wing will depend on where it is held by the beak. The closer to the apex (away from the base) the weaker the wing. The force applied on the wing by the struggling butterfly increases and the weight of the butterfly also starts to play a role in the process of tearing. I have in my collection of several thousand *Heliconius* (a genus with markedly elongated elegant wings) a great number of specimens with wing damage considered to be the result of a bird attack. Only in a few of them is the damage located in the space between Cu1 and 2A.

Under the conditions of the experiment the strength with which the artificial metal beak holds the wing of each tested dead butterfly remains constant. The initial reaction of the bird to the violent effort of the prey to escape from the grip of the beak is disregarded. If the insect manages to escape, it is usually immediately after being caught — a very dynamic event.

Obviously, if unpalatable butterflies have a high wtw in contrast to the low wtw of the palatable butterflies (DeVries 2002), the supposedly unpalatable models should also have a higher wtw in contrast to that of the palatable mimics. In DeVries (2003), an aposematic model (*Amaurus albimaculata*) was found to have significantly tougher wings than its putative Batesian mimic (*Pseudacraea lucretia*); the mimic was found to have significantly tougher wings than its non-mimic relative, a palatable species belonging to a different genus (*Cymothoe herminia*). Note that the experimental design used to measure the wing tear weights is the same in both papers. No doubt, the results of the experiments performed in both papers will be the same, and the conclusions also. The only difference between the two papers is that *only one* species of unpalatable butterfly considered the model was tested against *only one* species considered a putative mimic (a palatable butterfly) and one non-mimic palatable butterfly (2003), instead of the two palatable and three unpalatable species, again belonging to different genera, but not considered models and mimics (2002).

If mimics have higher wtw than non-mimics, all mimetic butterflies in the genus should have higher wtw than the non-mimics in the same genus. Mean wtw differed significantly among different individuals

of the species tested. Figure 1 of DeVries (2002) shows that the highest wtw of *P. lucretia* (N = 23) was far above the lowest wing tear weight of *A. albimaculata*. The same was found for the wing tear weight of *C. herminia* (N = 14) compared to that of *P. lucretia*. Does this marked amplitude between the highest and the lowest wtw in different individuals belonging to the same species indicate differences in toughness of their wings? Different distastefulness? If there is a corollary between wtw and palatability, there should be a significant difference in palatability and flight pattern among individual species (mimetic and non-mimetic) belonging to the same genus. I do not know a butterfly genus comprising species morphologically different or with different flight patterns. Why would mimetic species have a higher wtw than non-mimetic species belonging to the same or different genera? Is there a corollary between wtw and the ability of a species to mimic a model? Is a certain level of wtw necessary to enable a species to mimic a model?

DeVries states that his method provides a means for asking whether model butterflies are tougher than mimics, and if non-mimic butterflies are the weakest ones. He also states that "by exploring the parallel between the palatability spectrum and wing toughness we may potentially open new horizons in the evolution of bad taste." Obviously, I fully disagree! I consider the results obtained by DeVries (2002, 2003) an experimental artifact. The conclusions drawn are valid only for the conditions of the experiment. They cannot, and should not, be extrapolated to the different conditions existing during an attack of a bird on a butterfly in nature.

LITERATURE CITED

- CHAI, P. 1986. Field observation and feeding experiments on the response of Rufous Tailed Jacamars (*Galbula ruficunda*) to free-flying butterflies in a tropical rainforest.
- . 1988. Wing coloration of free-flying Neotropical butterflies as a signal learned by a specialized avian predator. *Biotropica* 20: 20-30.
- and R. B. Srygley. 1990. Predation and the flight, morphology, and temperature of Neotropical rain-forest butterflies. *Am. Nat.* 135: 748-765.
- COTT, H. B. 1940. Adaptive coloration in animals. Methuen, London.
- DEVRIES, P. J. 2002. Differential wing toughness in distasteful and palatable butterflies: direct evidence supports unpalatable theory. *Biotropica* 34: 176-181.
- . 2003. Tough African models and weak mimics: new horizons in the evolution of bad taste. *J. Lepidopterists' Soc.* 57: 235-238.
- EDMUNDS, M. 1974. Defence in Animals: A survey of antipredator defences. Longman, Burnt Mill.
- ELLINGTON, C. P. 1991. Limitation on animal flight performance. *J. Exp. Biol.* 160: 71-91.
- HOCKING, B. 1958. Insect flight. *Sci. Am.* 199: 92-95.
- KASSAROV, L. 1999. Are birds able to taste and reject butterflies based on "beak mark tasting"? A different point of view. *Behaviour* 136: 965-981.
- . 2003a. Notes on the evolution of unpalatability in butterflies by means of individual selection. *J. Res. Lepid.* 37: 71-73.
- . 2003b. Are birds the primary selective force leading to evolution of mimicry and aposematism in butterflies? An opposing point of view. *Behaviour* 140: 433-451.
- . 2003c. Is aposematism a valid concept in predator-prey relationship between birds and butterflies? A different point of view. *Tropical Lepid.* 2003, in press.
- MARSHALL, G. A. K. 1909. Birds as a factor in the production of mimetic resemblance among butterflies. *Trans. Roy. Entomol. Soc. Lond.* 1909:329-383.
- PINHEIRO, C. E. G. 1996. Palatability and escaping ability in Neotropical butterflies: Tests with wild kingbirds (*Tyrannus melancholicus*, Tyrannidae). *Biol. J. Linn. Soc. Lond.* 59: 351-365.
- SRYGLEY, R. B. & P. CHAI. 1990. Flight morphology of Neotropical butterflies: palatability and distribution of mass to the thorax and abdomen. *Oecologia* 84: 491-499.
- SRYGLEY, R. B. 1994. Locomotor mimicry in butterflies? The association of position of centers of mass among groups of mimetic unprofitable prey. *Phil. Trans. Roy. Soc. Lond. (B)*, 343: 145-155.
- WIKLUND, C. & T. JÄRVI. 1982. Survival of distasteful insects after being seized by naïve birds. A reprisal of the theory of aposematic coloration evolving through individual selection. *Evolution* 36: 998-1002.

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